Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics

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Summary

1. Throughout much of Britain, Ireland and north Italy, red squirrels (*Sciurus vulgaris* L.) have been replaced by alien grey squirrels (*S. carolinensis* Gmelin) introduced from North America. We have studied squirrels in two mixed woodlands in north Italy and two conifer forests in north England. In each country, one site was occupied by red squirrels and one site by both species.

2. We have previously considered interference competition and exploitation competition for food and space between red and grey squirrels and have showed that grey squirrels caused reduced body growth in juvenile and subadult red squirrels, and compete for tree seeds cached by adult red squirrels in spring. Here we report on the effects of grey squirrels on three fitness components in red squirrels that have consequence at the population level: fecundity, residency and recruitment.

3. Litter production peaked in the spring and summer, but fewer females bred in the summer with grey squirrels present. In addition, fewer individual red squirrel females produced two litters per year in the sites with grey squirrels. Moreover, red squirrel recruitment rate and, in the mixed broadleaf sites, red squirrel juvenile residency, decreased with increasing grey squirrel density.

4. Fecundity of individual female red squirrels was lower in red–grey than in red-only sites because they had a lower body mass in sites with grey squirrels.

5. Overall, there was no significant effect of grey squirrels on residency of adult red squirrels or on population turnover rate. However, the presence of grey squirrels resulted in a reduction in red squirrel fitness which was evident by lower population summer breeding and a lower recruitment. Over time, this will result in a decline in population size and eventually population extinction.

Key-words: demographic processes, fecundity, invasive species, *Sciurus carolinensis*, *Sciurus vulgaris*.

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Introduction

When resource availability is limited, one organism will have negative effects upon another by controlling access to, or by consuming, this resource. This definition of competition by Keddy (1989), implies that (1) an important resource must be limited for competition

to occur, and (2) the effects of competition operate primarily on the individual. Thus, at the level of the individual, it can affect reproduction negatively (e.g. delayed reproduction and/or reduced reproductive output in a single year, resulting in a lower lifetime reproductive success), survival, dispersal (increase the likelihood that an individual will leave a site) and niche use or habitat selection (reduced access to high quality habitats or resources, e.g. Wauters, Lurz & Gurnell 2000; Wauters *et al*. 2001a). These effects on the individual will be translated into effects at the population

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level by adversely affecting one or more population processes, reproduction, survival or recruitment of immigrants and/or locally born juveniles, which will result in reduced per capita growth rate for a given density. Such intraspecific competitive effects within populations of red squirrels (*Sciurus vulgaris* L.) have been demonstrated from studies in Belgium (e.g. Wauters & Dhondt 1989, 1993, 1995; Wauters & Lens 1995). However, noticeably, nothing has been published on similar interspecific competitive effects in tree squirrels.

It is well known that the coexistence of potentially competing species is possible by niche differentiation (e.g. Emmons 1980; Riege 1991; Brown, Kotler & Mitchell 1994). However, new species introduced artificially into ecosystems pose a particular problem because there may not have been sufficient 'evolutionary' time for niche differentiation to occur. Thus competitive exclusion might take place. The wide-scale replacement of the native Eurasian red squirrel throughout the British Isles and parts of northern Italy by the North American grey squirrel (*Sciurus carolinensis* Gmelin) is a well-documented example of an invasion by an alien species with the concomitant loss of a native species (Gurnell & Pepper 1993; Lurz *et al*. 2001). Until recently, the mechanisms of competitive replacement of red by grey squirrels were little understood (see Gurnell 1987). Although there is no evidence of interference competition between adults of the two species (Wauters & Gurnell 1999), body size may represent a correlated asymmetry that determines the outcome of interactions between individuals of the two species without overt aggression. Body size and age are believed to play such a role in intraspecific interactions and the establishment of social hierarchies within each species (Thompson 1978; Allen & Asprey 1986; Gurnell 1987; Wauters & Dhondt 1989, 1993, 1995; Wauters *et al*. 1995a).

There is evidence that grey squirrels are more efficient at exploiting acorns than red squirrels (Kenward & Holm 1989) because they are physiologically more adept at neutralizing acorn phytotoxins (Kenward & Holm 1993). Breeding and survival of grey squirrels respond positively to the size of acorn crops (Gurnell 1996a) and it is possible that feeding competition largely explains the replacement of red by grey squirrels in forests dominated by oak trees (Kenward & Holm 1989). However, this is not the case in other types of forest, such as conifer forests (Gurnell 1996b), and the food exploitation hypothesis has generally been discounted as a universal explanation (Wauters *et al*. 2001a). In a similar vein, it has been pointed out that grey squirrels put on more body mass in autumn than red squirrels (Kenward & Tonkin 1986), which enhances grey squirrel overwinter survival and the probability of breeding the following spring. However, this autumn increase in body mass does not occur in all years (Gurnell 1996a) or habitats (Lurz & Lloyd 2000). In particular, fat accumulation is likely to be less marked in conifer habitats where autumn and winter

food supplies are more predictable and manoeuvrability in the canopy may be important.

Another hypothesis is that competition between the two species is mediated by disease that results from parapoxvirus infection (Rushton, Lurz & Gurnell 2000). Grey squirrels are believed to be carriers of parapoxvirus in the United Kingdom and, although the virus has no affect on grey squirrels, it causes a disease that is invariably fatal in red squirrels (Tompkins *et al*. 2002). Thus, it appears that parapoxvirus can result in the loss of local populations of red squirrels which may influence the rate and extent of the ecological replacement of red by grey squirrels (Gurnell & Mayle 2003). However, there is no evidence that parapoxvirus occurs in red or grey squirrels in Italy (Luc Wauters and Alessandra Scagliarini, unpublished) where grey squirrels are expanding their range and replacing red squirrels (Lurz *et al*. 2001; Bertolino & Genovesi 2002).

Our studies on red squirrel–grey squirrel competition in Britain and Italy have examined the effects of grey squirrels on the behaviour, diet choice, use of cached tree seeds, habitat use and body growth of individual red squirrels (Wauters & Gurnell 1999; Wauters *et al*. 2000, 2001a; Wauters, Tosi & Gurnell 2002a). As mentioned above, we found no evidence of interference competition between the adults of the two species (Wauters & Gurnell 1999) or food competition (Wauters *et al*. 2001a) from our studies in England and Italy. However, we have shown that the growth rate of young red squirrels is slightly lower when grey squirrels are present and suggested that red recruitment is lower (Wauters *et al*. 2000). Moreover, co-occurring red and grey squirrels in deciduous woodlands show no important niche partitioning (Wauters *et al*. 2002b) and grey squirrels pilfer the seed caches of red squirrels in areas of overlap during the spring, leading to a lower red squirrel body mass at this time of the year, which could subsequently affect their reproductive success (Wauters *et al*. 2002a).

In this paper, we investigate the population dynamics of red squirrels in our study areas in the two countries with and without grey squirrels present. In particular, we ask whether grey squirrels affect red squirrel fecundity at the individual level, and then how red squirrel breeding rate, recruitment rate and residency are influenced by the presence of its congener.

Methods

STUDY DESIGN

The study design comprised two experimental 'red–grey' sites (with both red and grey squirrels present), one in northern Italy, Borgo Cornalese, Piedmont (RG1, 13 ha, 44°55′ N, 7°44′ E) and one in northern England, Hamsterley Forest, County Durham (RG2, 2000 ha, 54°40′ N, 1°55′ W), and two control 'red-only' sites (sites with only red squirrels), again one in northern Italy, Parco Pineta, Lombardy (RO1, 3000 ha,

Table 1. Trapping, food abundance and red squirrel population density data for the four study sites. RO1 = red-only site in Italy, RG1 = red–grey site in Italy, RO2 = red-only site in England, RG2 = red–grey site in England, FOOD = estimates of total annual seed production expressed as min and max MJ ha^{-1} (1 MJ = 10^3 kJ) for the periods of study, PRB = prebreeding density in late autumn-winter, POB = post-breeding density in summer, AF density = adult female prebreeding density, AF body mass = mean summer–autumn body mass (SD) of adult females.

Study site	Trapping period	Trap grid size (ha) and (traps ha^{-1} in brackets)	FOOD (MJ ha^{-1}) min to max	Squirrel density (ha^{-1}) PRB to POB	AF density PRB (ha^{-1})	AF body mass (g)
RO1	July 96–October 99	22 (1·3)	6804–10 943	0·39–0·58 to 0·71–0·90	0·23–0·32	326 (22)
RG1	July 96–November 98	13 (1·6)	3375–8 125	1·00–1·62 to 1·85–2·31	0·46–0·77	310 (22)
RO2	January 92–October 94	58 (0·5)	22–42	0·17–0·22 to 0·21–0·24	0·09–0·12	308 (20)
RO2	April 97–November 98	41 (0·9)	26–36	0·29 to 0·36–0·46	0·20	314 (15)
RG2	April 97–November 98	27 (0·9)	74–213	0·26 to 0·33–0·37	0·18	291 (17)

45°45′ N, 8°57′ E) and one in northern England, Spadeadam Forest in Kielder Forest, Cumbria (RO2, 5000 ha, 55°02′ N, 2°35′ W). The two English sites were at a slightly higher latitude than the Italian sites. However, the natural distribution of both species embraces a wide range of climatic zones, from the boreal forests in the north to Mediterranean habitats in the south (Corbet 1978) in the case of Eurasian red squirrels, and from the cold continental climate of Saskatchewan in the north to Florida in the south (Koprowski 1994) in the case of North American grey squirrels. All our sites fell within the more moderate range of climatic zones of the distribution of the two species. Moreover, there is no evidence of any systematic latitudinal effect on reproduction and survival in these species (e.g. see Gurnell 1987), and we believe our sites are valid replicates according to climate. In both Italy and England, we selected regions that were in the process of being colonized by grey squirrels.

The Italian sites were high-quality, mixed broadleaf and conifer woodlands with a high tree species diversity and a high food availability (see Wauters & Gurnell 1999; Wauters *et al*. 2001a,b; Table 1). The red-only study site in Parco Pineta was dominated by deciduous trees, mainly black locust (*Robinia pseudoacacia* L.), sweet chestnut (*Castanea sativa* Miller), oaks (*Quercus robur* L., *Q. petraea* Liebl.) and hornbeam (*Carpinus betulus* L.), with some 20% covered by Scots pine (*Pinus sylvestris* L.) and 17% by plantations of white pine (*Pinus strobus* L.) and Norway spruce (*Picea abies* Karsten). A diverse understorey consisted mainly of hazel (*Corylus avellana* L.) mixed with young deciduous trees with some elder (*Sambucus nigra* L.). The red–grey site was a mature, mixed deciduous woodland, dominated by oaks, hornbeam, field maple and sycamore (*Acer campestris* L., *A. pseudoplatanus* L.) and ash (*Fraxinus excelsior* L.). The walnuts of sparsely planted walnut (*Juglans regia* L.) and black walnut (*Juglans nigra* L.) were important food resources for both squirrel species. There was also a single block of planted white pine which covered about 8% of the study area. The dense understorey consisted of elder with some hazel (Wauters *et al*. 2001a,b).

In contrast, the English sites were typical of the region consisting of mixed aged conifer plantations with low tree species diversity (Wauters *et al*. 2000). The study site at Spadeadam Forest (red-only site) was planted with mature conifer trees (> 30 years old), Sitka spruce (*Picea sitchensis* Carr.), Norway spruce and lodgepole pine (*Pinus contorta* Dougl.) capable of cone production. Hamsterley Forest (red–grey site) was a mixed forest with deciduous trees in the valley bottoms and conifer plantations on the slopes higher up. In the past, red squirrels occurred throughout the forest. However, since the arrival of grey squirrels in the early 1980s the range of red squirrels contracted with the increase of the congener. At the time of the study they were found in low numbers only in the conifer plantations higher up on the hillsides. The study site consisted of some beech (*Fagus sylvatica* L.) a pure Scots pine stand, a mixed plantation of Sitka spruce with some Scots pine and a pure Sitka spruce stand (Wauters *et al*. 2000).

Because of these differences in forest structure and food supply, the two experimental and two control sites were not true replicates. However, the differences in forest composition allowed us to investigate whether effects of interspecific competition differed between co-occurring populations in mixed deciduous woodlands and in conifer forests.

FOOD ABUNDANCE ESTIMATES

Annual food supplies, the seed crop size of different tree species, were estimated by counting fallen cones on transect lines in the conifer sites (Lurz 1995; Wauters *et al*. 2000) and by counting fallen cones and seeds of broadleaf trees on 1-m^2 sampling plots in the mixed woodlands in northern Italy (Wauters *et al*. 2001a,b). To combine data of different tree seed species, the number of seeds m^{-2} were converted to energy values (kJ m^{-2}), using the mass-specific energy-content of the various seed species (kJ g^{-1}, Wauters *et al*. 2001a,b). Total food abundance (in 10^6 J ha^{-1}, Table 1) was calculated as the mean over all sampling plots or transect lines in the whole study site (Wauters *et al*. 2001b).

Table 2. Demographic parameters of red squirrels in the four study sites. Data are presented combining years (see Table 1), category = sex (residency), season (breeding rate, spring vs. summer breeding season), or sex–age category (recruits), % of each sex–age combination on total number of recruits within brackets. The *P*-values are from single factor *G*-values with William's correction of the log-linear models with d.f. = 1

Parameter	Category	Site RO1	Site RG1	Site RO2	Site RG2	Factor	*P*
Residency	Males	8/21 (38%)	14/21 (67%)	10/28 (36%)	3/6 (50%)	Site	0·11
	Females	18/27 (67%)	11/17 (65%)	14/27 (52%)	2/4 (50%)	Habitat	0·20
						Sex	0·06
Breeding rate	Season						
	Spring	18/25 (72%)	16/22 (73%)	22/39 (56%)	5/9 (56%)	Site	0·25
						Habitat	0·11
	Summer	13/22 (59%)	4/21 (19%)	14/28 (50%)	3/9 (33%)	Site	0·006
						Habitat	0·90
Litters/year	0	4 (17%)	3 (15%)	5 (22%)	1 (11%)		
	1	10 (42%)	16 (80%)	12 (52%)	8 (89%)		
	2	10 (42%)	1 (5%)	6 (26%)	0		
Recruits	Subad. males	7 (39%)	7 (44%)	5 (22%)	0		
	Adult males	4 (22%)	2 (12%)	8 (35%)	1 (50%)		
	Subadult fem.	5 (28%)	4 (25%)	3 (13%)	0		
	Adult females	2 (11%)	3 (19%)	7 (30%)	1 (50%)		

Seeds and fruits produced in the summer–autumn of year *t* were considered available for the squirrels during the following 'squirrel year' (see Wauters & Lens 1995), i.e. from July of year *t* to June of year *t* + 1.

TRAPPING AND HANDLING

All populations were studied using capture–mark–recapture techniques, combined with radio-tracking (e.g. Wauters & Gurnell 1999; Lurz, Garson & Wauters 2000), and population parameters were measured directly by monitoring marked and radio-tagged individuals (Table 2). In northern England, squirrels were trapped in spring (April–May) and autumn (September–October) of 1997 and 1998, and additional data were available for the red-only site for 1992–94 (Lurz 1995; Tables 1 and 2). In the Italian sites, squirrels were trapped bimonthly from July 1996 to November 1998 (red–grey site) or to October 1999 (red-only site). Traps were placed randomly or in a grid, on the ground or at a height of 1·5 m against tree trunks, prebaited for 5 days and set for 5–8 days (Wauters & Dhondt 1993; Lurz 1995). Each trapped squirrel was individually marked using numbered metal eartags (type 1003 S National Band and Tag Co, Newport, KY, USA), and weighed to the nearest 5 g using a Pesola spring-balance, and the length of the right hind foot (without the nail) was measured (0·5 mm) with a thin ruler (Wauters & Dhondt 1989; Wauters & Gurnell 1999). Sex, age and reproductive condition were recorded: subadult males are between 4 and 10 months old, with abdominal testes and a small scrotum; subadult females are between 4 and 10 months old, have a very small vulva, and the nipples are still invisible; adults are over 10–12 months old. Lactating females with enlarged nipples were considered breeding (Wauters & Lens 1995). We used the minimum number of animals known to be alive (MNA), from trapping, radiotracking and observations, at each

trapping period as our estimate of population size. Because high trapping success allowed us to tag most or all of the non-juvenile squirrels in all study sites, we feel confident that these estimates reflect red squirrel densities realistically (Table 1). In study sites RO1, RO2 and RG2, that were part of a larger forest, an edge correction of the trapping area of 100 m (study area extended 100 m beyond the area covered by the traps on all sides) was used to estimate densities (Wauters *et al.* 2001b). The length of the study period, study area size, trap density, size of the tree seed crop and red squirrel densities are summarized in Table 1.

POPULATION PARAMETERS AND STATISTICAL ANALYSES

Residents were adults and subadults present in October (RO2 and RG2 in 1997) or January–February (RO1, RG1 and RO2 in 1992–94) of each year that had been marked previously. New, unmarked squirrels (including locally born juveniles as well as immigrants, i.e. subadult or adult squirrels, born elsewhere) were defined as: (i) transients, when caught only in a single trapping session; or (ii) recruits, that stayed resident on the study area for at least 6 months. Thus, transients were squirrels that did not establish a home range and they were omitted from the analysis of population turnover. Because we could not always distinguish between mortality or emigration in those animals that disappeared, we defined losses as animals captured but not subsequently recaptured for six months or longer. Using the classes outlined above, we defined the percentage population turnover from year *t* to year *t* + 1 as: % turnover = [(no. of recruits + no. of losses)/no. of residents] × 100. There is increasing evidence that the two sexes of squirrels should be considered separately (e.g. with respect to space use, aggressive behaviour, dominance and the use of critical resources; Thompson

Table 3. Yearly recruitment and turnover rate (%) of male and female red squirrels in relation to the density of grey squirrels of the same sex at red–grey sites RG1 = deciduous site; RG2 = conifer site

Site	Year	Sex	Grey squirrel density	Red squirrel recruitment	Red squirrel turnover rate (%)
RG1	1996	Male	0·46	0·95	129
		Female	0·15	0·71	114
RG1	1997	Male	0·69	0·15	46
		Female	0·54	0·22	56
RG2	1997	Male	0·62	0·20	80
		Female	0·52	0·25	75

1978; Allen & Aspey 1986; Wauters & Dhondt 1989, 1992, 1993; Wauters & Lens 1995) and we use male and female densities in our analyses.

Residency (from year t to year $t + 1$) was estimated as the ratio of the number of animals present in October–November of year t and still alive in October $t + 1$ to the number of animals present in October of year t. Recruitment rate was calculated as the number of recruits per resident present in October of each year (after Wauters *et al.* 1994).

Breeding success was calculated as the proportion of adult females that were lactating, for spring and summer breeding seasons separately. When so-called 'intermediate litters' occurred, with parturition between mid-April and mid-June, the litter was assigned to spring litters when born before mid-May, and to summer litter when born after mid-May (Table 2). The period of natal dispersal, which occurs between 4 and 10 months old, is a critical period in the life cycle of red squirrels, with high mortality in juveniles and sub-adults in poor condition and in offspring of mothers of low body mass (Wauters & Dhondt 1993; Wauters, Bijnens & Dhondt 1993). We estimated juvenile survival rates, or residency as we have termed it, as the number of juveniles and subadults recruited from July of year t to June $t + 1$ divided by the number of potentially weaned juveniles from spring and summer litters of year t. We obtained the latter by extrapolation from the estimated number of weaned juveniles, which was calculated by multiplying mean litter size at weaning with the number of litters (Table 3). In all study sites except RG2, a large proportion of lactating females was fitted with radio-collars to locate breeding nests, and litter size at weaning was determined by marking young in the nest (at 3–5 weeks old) or by trapping and observing young near the nest tree (Wauters *et al.* 1993; Wauters & Lens 1995). Mean litter size at weaning was 1·78 young/litter ($n = 9$) in site RO1, 2·0 ($n = 6$) in RG1 and 2·75 ($n = 4$) in RO2. In the red–grey site in northern England (RG2), it was estimated at 1·5 young/litter (according to Wauters *et al.* 2000). Fecundity of individual, adult female red squirrels has been defined as the number of breeding events divided by the number of breeding seasons that a female was present in the study site, after Wauters *et al.* (2001b).

To compare residency and breeding success between red-only and red–grey sites (factor site), taking into account potential habitat effects (factor habitat: conifer forests in England vs. broadleaf woodlands in Italy) and sex-effects (factor sex: males vs. females) or season effects (factor season: spring vs. summer breeding), we used hierarchical log-linear models with William's correction for small sample size (Sokal & Rohlf 1995). Elsewhere, we showed that there was no statistically significant period effect (1992–94 vs. 1997–98 data) on the proportion of breeding females and on residency in site RO2 (all $P > 0·1$, Wauters *et al.* 2000). Hence, to increase sample sizes in site RO2, data were pooled over both periods. When testing for intraspecific density-dependence, the densities of male and female red squirrels were considered separately. The demographic parameters, annual recruitment rate, turnover rate and the number of transients ha^{-1} were used as dependent variables in multiple analysis of covariance (ANCOVA) models ($n = 20$) with density of red squirrels of the same sex (males ha^{-1} or females ha^{-1}) as the independent variable, and habitat, site and sex as factors. All means are presented ± 1 standard deviation (SD), unless noted otherwise.

Results

None of the log-linear models had a significant three-way habitat by site by sex interaction (all $P > 0·25$). Residency tended to be higher in adult females than in adult males in the red-only sites, but the site × sex interaction ($G_1 = 1·71$, $P = 0·19$) and the sex effect were not significant (Table 2). There was no significant effect of habitat or site on residency of adults (Table 2).

Breeding rate had a significant site × season interaction and a significant season effect (interaction $G_1 = 5·09$, $P = 0·02$; season $G_1 = 7·87$, $P = 0·005$). Therefore, habitat and site effects were investigated for spring and summer breeding separately, using two-way G-tests. In spring, none of the factors affected breeding rate significantly, but summer breeding rate was higher in the red-only than in the red–grey sites (Table 2). Thus the breeding rate of female red squirrels in summer was reduced when grey squirrels were present. Because each female red squirrel can produce no, one or two litters per year, we also tested for a habitat and site effect on the proportion of adult females producing different number of litters (Table 2). These proportions differed significantly between red-only and red–grey sites, but not between habitats (site effect $G_2 = 13·4$, $P = 0·0014$;
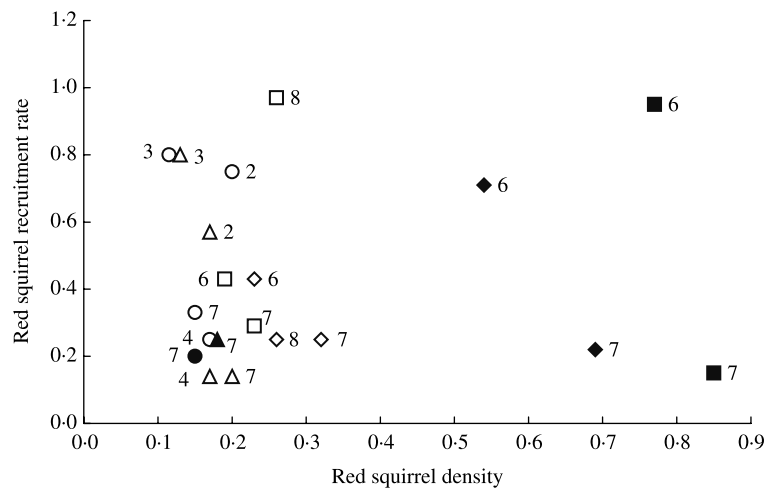
Fig. 1. Yearly recruitment rates of male and female red squirrels in relation to red squirrel density of that sex (no. ha^{-1}), site (red-only vs. red–grey sites), habitat (conifers in northern England vs. deciduous woods in northern Italy) and sex (males vs. females). Open squares: males in RO1 (red-only deciduous); open diamonds: females in RO1; full squares: males in RG1 (red–grey deciduous); full diamonds: females in RG1; open circles: males in RO2 (red-only conifer); open triangles: females in RO2; full circle: males in RG2 (red–grey conifer); full triangle: females in RG2. The label next to each point refers to the year in the 1990s, e.g. 6 = 1996.
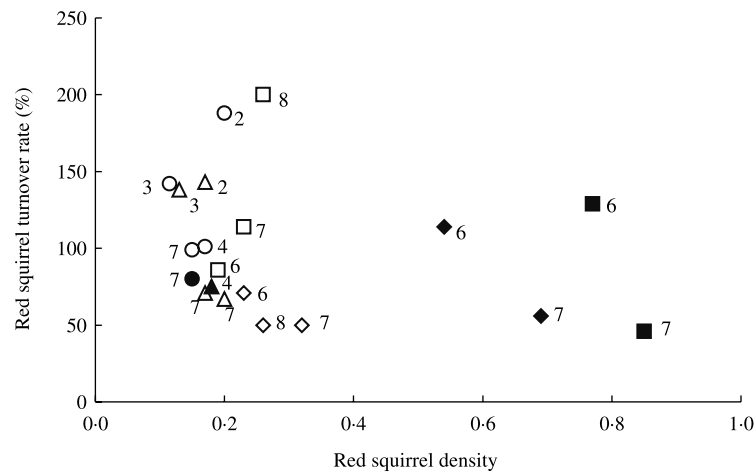
Fig. 2. The relationship between turnover rate of male and female red squirrels and red squirrel density, site, habitat and sex. Open squares: males in RO1 (red-only deciduous); open diamonds: females in RO1; full squares: males in RG1 (red–grey deciduous); full diamonds: females in RG1; open circles: males in RO2 (red-only conifer); open triangles: females in RO2; full circle: males in RG2 (red–grey conifer); full triangle: females in RG2. The label next to each point refers to the year in the 1990s, e.g. 6 = 1996.

habitat effect $G_2 = 1·72$, $P = 0·44$). There were higher proportions of adult females with two litters per year in the red-only than in the red–grey sites (Table 2). The habitat × site interaction was not significant ($G_1 = 2·63$, $P = 0·11$), indicating that the differences between red-only and red–grey sites were consistent for both the conifer and broadleaf habitats. These data agreed with reduced summer breeding by red squirrels in sites where both squirrel species coexist.

Red squirrel recruitment rates (Fig. 1) were independent of red squirrel density, and there was no significant effect of site (red-only vs. red–grey site), habitat or sex (ANCOVA, effect of density of red squirrels of same sex $F = 0·01$, $P = 0·99$; site effect $F = 0·12$, $P = 0·74$; habitat effect $F = 0·11$, $P = 0·74$; sex effect $F = 0·90$, $P = 0·36$, d.f. = 1,15 in all cases). The age compo-

sition of recruits differed between habitats, with a higher proportion of adult recruits in conifer sites (Table 2, deciduous sites 67% subadults and 33% adults; conifer sites 32% subadults and 68% adults; Fisher's exact test, $P = 0·007$), but there was no significant difference in the proportion of adults among recruited red squirrels between red-only and red–grey sites in either habitat (Table 2, Fisher's exact tests, deciduous habitat $P = 0·59$, coniferous habitat $P = 0·45$). However, recruitment of red squirrels decreased with increasing grey squirrel density of the same sex in the red–grey sites (Table 3, $r_s = -0·94$, $P = 0·005$, $n = 6$).

Percentage turnover rate did not differ significantly according to site and habitat and was not related to red squirrel density (ANCOVA, all $P > 0·4$, Fig. 2). It tended to be higher in male than in female red squirrels
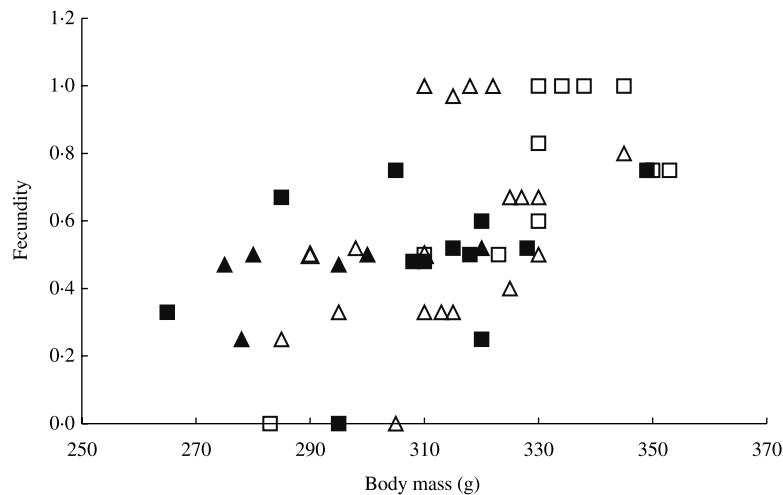
Fig. 3. Correlation between female red squirrel fecundity and body mass, according to site (red-only vs. red–grey sites) and habitat (deciduous vs. conifer forests). Open squares: individual females from site RO1 (red-only deciduous); full squares: from site RG1 (red–grey deciduous); open triangles: from site RO2 (red-only conifer); full triangles: from site RG2 (red–grey conifer).

Table 4. Estimates of the number of weaned offspring, from the number of litters produced (between brackets) and of juvenile residency (proportions within brackets)

Parameter	Year	Site RO1	Site RG1	Site RO2	Site RG2
Weaned offspring	1992–94			47 (17)	
(number of litters)	1996–97	16 (9)	14 (7)		
	1997–98	20 (11)	16 (8)	11 (4)	8 (5)
Juvenile residency	1992–94			10 (0·21)	
	1996–97	6 (0·38)	7 (0·50)		
	1997–98	5 (0·25)	2 (0·13)	3 (0·27)	1 (0·13)

(ANCOVA, sex effect $F_{1,15} = 3·16$, $P = 0·096$) and in a pairwise comparison (i.e. male vs. female turnover rate in the same site, habitat and year), male turnover was significantly higher than that of females (Wilcoxon matched-pairs signed-ranks test $N = 9$, $T = 2$, $P = 0·01$). Red squirrel turnover rate per sex was not correlated significantly with density of grey squirrels of the same sex (Table 3, $r_s = -0·77$, $P = 0·07$, $n = 6$).

The number of male and female red squirrel transients ha^{-1} increased with density of red squirrels of the same sex (ANCOVA, density effect $F_{1,15} = 4·70$, $P = 0·047$), but did not differ according to site, habitat or sex (all $P > 0·2$). This indicates indirectly intraspecific effects on recruitment in red squirrels. The estimated juvenile residency (Table 4), combined over all years, did not vary with habitat type or between red-only and red–grey sites (two-way G-test: habitat × site interaction $G_1 = 0·31$; habitat effect $G_1 = 1·41$; site effect $G_1 = 0·12$, all $P > 0·2$). Interestingly, however, juvenile residency decreased from 1997 to 1998 in both broadleaf woodlands in N. Italy (Table 4), but this difference was only significant in the red–grey site where juvenile residency was reduced to only 13% in 1998 when grey squirrel numbers had increased twofold (Fisher's exact tests: RO1 $P = 0·48$; RG1, $P = 0·046$).

Fecundity of individual female red squirrels tended to be higher in the red-only than in the red–grey sites

$(0·62 \pm 0·30, n = 31$ vs. $0·48 \pm 0·18, n = 18)$, independent of the habitat (two-way ANOVA, site effect $F_{1,46} = 4·47$, $P = 0·04$; habitat effect $F_{1,46} = 1·60$, $P = 0·21$). However, when the effect of body mass was added, only variation in body mass significantly explained 32% of individual variation in female fecundity (Fig. 3, ANCOVA, effect of body mass $F_{1,44} = 15·3$, $P = 0·0003$), while the partial effects of site, habitat and the site × habitat interaction were not significant (Fig. 3, ANCOVA, all $P > 0·25$). This suggests that the effects of grey squirrels on red squirrel female fecundity maybe mediated through a lower female body mass. In the red–grey site in Italy (site RG1), where there was a high degree of individual variation in the amount of core-area overlap of female red squirrels with grey squirrels (Wauters *et al.* 2002b), fecundity of female red squirrels tended to decrease with increasing interspecific core-area overlap ($r = -0·56$, $P = 0·076$, d.f. = 9).

Discussion

THE STUDY DESIGN

The carrying capacity of both squirrel species differed markedly between man-made conifer plantations (low) and mixed deciduous woods (high), and this is likely to affect the intensity of interspecific competition and

therefore the duration of coexistence before red squirrels are completely replaced by grey squirrels at each site. At Hamsterley (site RG2), for example, both species were still present 16 years after the first grey squirrels colonized the forest. In contrast, at Racconigi, a deciduous woodland that was similar in tree species composition and tree seed abundance to our study site RG1, red squirrels went extinct in 1997, only 8 years after the first grey squirrels were observed (Sandro Bertolino, personal communication). In this woodland of 70 ha, grey squirrels densities in 1996 were high (prebreeding density five animals ha^{-1}), and red squirrels became very rare with no animals trapped during 2 years of live trapping. Hence, the Racconigi site could not be used as a red–grey replicate for site RG1 and demonstrates the difficulties of site replication in experimental field studies.

To minimize the effects of the lack of true site replication, we have tested for a 'habitat' effect (conifers vs. broadleaf, thus English vs. Italian sites) in all analyses, and for interactions of habitat with the other factors. Because habitat effects or interactions with habitat were not significant for any of the population processes examined, we feel confident that our results enable us to draw some general conclusions about demographic consequences of interspecific competition between red and grey squirrels.

The size of tree seed crops of both conifers and most broadleaf trees show strong annual fluctuations. These affect reproduction, survival and dispersal of individual squirrels, and thus density and growth rate of tree squirrel populations (e.g. Gurnell 1987, 1996a; Wauters & Dhondt 1995; Wauters & Lens 1995; Lurz *et al*. 1997, 2000). Thus critical resources will not be limiting in all years and competition will occur when food supplies (per animal) become insufficient to support all individuals. As a consequence, the effects of both intra- and interspecific competition will be difficult to reveal, or even be non-existent, in some years but pronounced in others. This makes it difficult to demonstrate such effects in short-term studies such as ours, and indicates the need for relatively long-term studies with sufficient replicates (study sites). In addition, grey squirrel densities in our experimental sites were still low, especially in site RG1 (Wauters & Gurnell 1999; Wauters *et al*. 2000; Gurnell *et al*. 2001), making our conclusions on possible interspecific competition effects conservative. Despite these potential problems, we found several biologically significant effects of the presence of grey squirrels on, for example, demographic processes in co-occurring red squirrels, that suggest the possible mechanisms of replacement competition.

CHANGES IN RED SQUIRREL POPULATION DYNAMICS WHEN GREY SQUIRRELS ARE PRESENT

Although there was no difference in the proportion of females breeding in the spring, our data show that rela-

tively fewer females bred in the summer in the red–grey sites than the red-only sites, even though we acknowledge that the sample size for the English red–grey site was low. Also, fewer individual females produced two litters in both red–grey sites than the red-only sites. Thus there was a reduction in summer breeding in sites where both species of squirrel were present compared to sites where only red squirrels were present, resulting in reduced fecundity of individual females. Both Lurz (1995) and Magris & Gurnell (2002) found that summer breeding in red squirrels increased when the females had access to supplementary food. Thus, lower summer breeding may result from a lower food availability relative to the number of squirrels present. This is supported by reduced fecundity of individual females caused by a decrease in body mass in the red–grey sites. We showed that in coexisting populations in northern Italy, grey squirrels pilfering red squirrels' food caches, caused a reduced energy intake in red squirrels with a high degree of interspecific core-area overlap, and a decrease of body mass in spring (Wauters *et al*. 2002a). Both in red squirrels and in American red squirrels (*Tamiasciurus hudsonicus* Erxleben), mass gain during lactation affects weaning success positively, and is an important component of parental investment (Wauters & Dhondt 1989; Humphries & Boutin 1996). Access to stored seeds was essential for individual female American red squirrels to increase their energy budgets, from slightly positive during early lactation to highly positive during late lactation (Humphries & Boutin 1996), while in female Eurasian red squirrels lifetime reproductive success increased with the amount of time spent feeding on cached seeds (Wauters, Suhonen & Dhondt 1995b). Hence, interspecific competition for scatterhoarded seeds could be the behavioural mechanism causing loss of body mass and reduced fecundity in adult females.

Two of the other population parameters we investigated, recruitment of red squirrels and estimated juvenile residency, suggest that interspecific competition increased when the numbers of grey squirrels increased overall animal densities. In all red–grey sites, red squirrel recruitment rate was density-dependent with grey squirrel density but not with red squirrel density. In other words, fewer male red squirrels were recruited into the study populations when the density of male grey squirrels increased, and fewer female red squirrels could settle in years or sites when the density of female grey squirrels increased. In fact, in the deciduous woodland in Italy, recruitment of red squirrels decreased significantly from 1997 to 1998 when the number of grey squirrels was increasing strongly (grey squirrel density in summer 1996 0·2 squirrels ha^{-1}, in summer 1997 0·9 ha^{-1}, and in summer 1998 1·92 squirrels ha^{-1}, resulting in per capita population growth-rate = 1·43 in 1996–97, and 2·50 in 1997–98, Gurnell *et al*. 2001). Recruits consisted of locally born juveniles and subadult and adult immigrants.

There were proportionally more adult recruits (both sexes combined) in the conifer forests in northern

England: 68% against only 32% adults in the deciduous woodlands in northern Italy. This was not surprising, as breeding dispersal among adult red squirrels (i.e. adult females leaving the home range where they reproduced after the breeding period), as well as emigration in response to temporal and spatial variation in food availability, was common in the spruce-dominated conifer plantations (Lurz *et al.* 1997, 2000). In contrast, in so-called 'stable' habitats where food availability is more predictable in space and time, it is juvenile and subadult red squirrels that tend to disperse whereas adults, especially females, have a high degree of site-fidelity (Wauters & Dhondt 1993; Wauters *et al.* 1995a; Lurz *et al.* 1997). Thus, we believe that dispersal behaviour and the age composition of recruits of red squirrels was determined mainly by patterns of resource availability, and less by the presence/absence of the congener.

Grey squirrel densities, however, did affect the number of juveniles and subadults that settled in the mixed-species sites, causing a decrease in red squirrel recruitment rate with increasing grey squirrel density. The effect of grey squirrels on residency in juvenile red squirrels was density-dependent. In site RG1, no reduced residency was observed in 1997, when grey squirrels still occurred at low densities (0.9 ha^{-1} in June 1997), but decreased drastically, from 50% to only 13% in 1998, when concomitantly densities of grey squirrels strongly increased. In the red–grey conifer site, we had no data on litter size and used a very conservative (low) average litter size of 1.5 weaned young (Wauters *et al.* 2000) for extrapolating juvenile residency. In this case, juvenile residency of red squirrels was not significantly reduced in sympatry with its congener (13% in RG2 vs. 27% in RO2 in 1997–98, and 21% in 1992–94). If we used a mean litter size of 2.75 in the red–grey site, as was found in the red-only site, the estimated juvenile residency was even lower (one of 14 young, 7%), but even this result was not significantly different from the estimated 21–27% in the red-only site (Fisher's exact test $P = 0.28$).

Conclusion

Our results indicate that the presence of grey squirrels leads to reduced red squirrel recruitment rates. Moreover, reduced juvenile residency of red squirrels occurs when grey squirrel densities increase, particularly in mixed deciduous woods. Similar patterns seemed to exist in conifer plantations, but these will need to be verified by more long-term data on the dynamics and behavioural ecology of sympatric red and grey squirrel populations. However, interspecific competition acting particularly on juvenile and subadult red squirrels is confirmed by our data on reduced body size, and thus reduced growth rate in red squirrels, in the red–grey sites compared to the red-only sites (see Wauters *et al.* 2000, 2001a). Together with the reduction in red squirrel summer breeding rate when both species are present, these results suggest that native red squirrels will almost

inevitably be excluded from deciduous woods by the alien species. We did observe grey squirrel impacts on red squirrel fecundity and recruitment in conifer habitat as well. However, we believe the outcome of competition in these woodlands is likely to depend on landscape structure (e.g. presence of areas of broadleaf habitat) and factors that influence dispersal behaviour such as spatial and temporal variations in habitat quality and food availability. To test these ideas, the next step would be to adopt an experimental approach by manipulating the numbers of greys present in mixed species sites within different habitat types and monitoring the effects on red squirrels.

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